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The effects of attenuating returning echolocation signals at the lower jaw of a dolphin (*Tursiops truncatus*)

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Recordings were made during an echolocation experiment in order to observe any changes in the parameters of outgoing signals as a function of the deliberate attenuation of returning signals at the lower jaw of a dolphin (*Tursiops truncatus*). A dolphin was conditioned to perform a discrimination task while wearing either of two rubber hoods covering its lower jaw in addition to performing the same task while wearing no hood. A control hood, made of gasless neoprene, allowed returning acoustic signals to pass to the lower jaw. An experimental hood, made of closed-cell neoprene, significantly attenuated such signals. As previously reported (Brill *et al.*, 1988), the dolphin's ability to echolocate was significantly hindered while wearing the experimental hood. The acoustical data we recorded during that experiment suggest that the use of the hoods did not affect the dolphin's ability to emit useful echolocation signals. The dolphin appeared to vary the temporal parameters of its emitted signals in terms of lower click repetition rates in both the control and experimental conditions and interclick intervals (ICIs) of shorter duration in the experimental condition. The lower repetition rates and shorter ICI's in the latter condition are attributed to the attenuation of returning echoes at the dolphin's lower jaw. The results support the theory that returning echolocation signals are best received along the lateral sides of the dolphin's lower jaw.

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INTRODUCTION

Norris (1964, 1968, 1969) hypothesized that returning echolocation signals are guided to the inner ear of odontocete cetaceans via areas of fatty tissues and thin bone on the lateral sides of the lower jaw and the associated mandibular fat body. This fat body fills the hollow mandible and attaches to the auditory bulla. According to Norris' theory, returning signals pass most easily through a thin oval-shaped area of fat on the lower jaw. This "acoustic window," devoid of muscle fibers, overlies the thinnest area on posterior end of the jaw bone. Once through the bone, signals enter the mandibular fat body, which is well differentiated from its surrounding tissues, and are guided to the thinnest area on the tympanoperiotic bone housing the structures of the middle and inner ears (Norris, 1968).

The "jaw-hearing" theory, as it has come to be informally called, is supported by a good deal of evidence despite the criticism of Purves and Pilleri (1983) that it is based on anatomical inference rather than experimental proof. The electrophysiological investigations of Bullock *et al.* (1968) and McCormick *et al.* (1970) demonstrated that the lateral sides of the dolphin's lower jaw were the primary sites of sound reception. Varanasi and Malins (1971, 1972) described lipid patterns unique to the melon and mandibular

fat bodies in odontocete cetaceans which they proposed would allow signals to pass between seawater and tissue with relatively little loss of energy. The biochemical composition of these fatty tissues of the lower jaw implicated in sound reception, while similar to that of the melon, is distinct from other fat stores in the body of the dolphin (Litchfield *et al.*, 1975). Norris and Harvey (1974) demonstrated passive sound transmission through the jaws and throats of recently dead odontocete cetaceans. However, the theory lacked evidence gained from a dolphin actively echolocating and listening under controlled conditions.

Brill *et al.* (1988) demonstrated that placing a sound-attenuating covering over the lower jaw significantly hindered a dolphin's (*Tursiops truncatus*) ability to echolocate. The dolphin was required to perform an echolocation discrimination task under three test conditions: (1) with no covering over the lower jaw (baseline), (2) with a covering, or hood, over the lower jaw that allowed returning echolocation signals to pass (control), and (3) with a hood over the lower jaw that significantly attenuated returning signals (experimental). The dolphin's performance was significantly hindered while wearing the sound attenuating hood over its lower jaw, as compared to the baseline (no hood) and control-hood conditions. Likewise, the difference in performance between trials conducted with and without a hood within the experimental condition was significant.

Characteristics of the dolphin's outgoing signals recorded during the experiment conducted by Brill *et al.* (1988)

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and analyzed by us are reported in this paper. Our purpose was to (1) determine if the dolphin's outgoing signals were disrupted by covering the lower jaw and (2) to establish whether or not the dolphin adjusted the parameters of its own signals in response to the test conditions.

I. METHOD

The apparatus and procedures used in this experiment have been previously described (Brill, 1988a, 1988b; Brill *et al.*, 1988).

Recordings were made in the shallow end of a 30.48 m \times 7.62 m \times 5.18 m concrete pool. The water was approximately 1.68 m deep and the dolphin could be stationed over the edge of a slope that led down to the deep center of the pool (Fig. 1).

The hoods, described by Brill (1988b) and Brill *et al.* (1988), were designed to cover the lower jaw from the tip of the snout to just a few centimeters anterior to the base of the pectoral fin along the line of the gape of the mouth. The hoods did not cover the area about the external auditory meatus. They were held in place by rubber straps and small suction cups. The hood used in the control condition was made of 0.16-cm thick gasless neoprene (*Durometer* purchased from the Abbott Rubber Co., 2143 Lunt Ave., Elk Grove Village, IL 60007). The hood used in the experimental condition was made from 0.48-cm closed-cell neoprene.

Tests to determine the attenuation values of the neoprene materials used were conducted in a concrete pool designed for making underwater acoustical measurements at

the Naval Ocean Systems Center in Kaneohe, Hawaii prior to beginning the experiment. An ARL-90 element planar transducer was mounted 1.8 m below the surface of the water. A Clevite CH-24 transducer was mounted in line with the ARL-90 at a distance of 2.1 m. Test signals were broadcast through the CH-24. The peak-to-peak amplitudes of the signals received with and without a neoprene covering placed over the ARL-90 were compared for the respective materials. Using simulated dolphin echolocation clicks, damped sinusoids 50 μ s in duration consisting of 5 cycles, it was determined that the gasless neoprene had attenuation values of 2.2 and 1.2 dB for signals with peak frequencies of 35 and 110 kHz, respectively. The closed-cell neoprene had attenuation values of 39 and 36 dB for signals with peak frequencies of 55 and 115 kHz, respectively (Au, personal communication).

The dolphin's outgoing signals, as it echolocated on a target, were recorded in all trials of a total of fourteen randomly selected sessions, each consisting of twenty trials, in each of the three conditions tested; four sessions in the baseline condition, five in the control condition, and five in the experimental condition. (The order in which the sessions were recorded is shown in Figs. 3-5.) An Edo-Western 6166 hydrophone was positioned directly over the dolphin's head on an underwater hoop station. A Celesco LC-10 hydrophone was placed 61 cm below the surface of the water, in line with the center of the hoop, and 1 m in front of the hoop station (see Fig. 1). Signals received by each hydrophone were amplified with 40 dB of gain, bandpass filtered between 3 and 200 kHz through Krohn-Hite 3550 variable filters, and recorded on separate channels of an Ampex FR-1300 portable instrumentation tape recorder operating at 152.4 cm/s providing a bandwidth of 280 kHz. To facilitate analysis, recordings were reduced by a speed factor of 16 and transferred to a Marantz PMD 360 stereo cassette tape recorder. Signal analysis was conducted on a Masscomp computer system. The analog recordings were transferred at an A to D conversion rate of 40 000 pts/s and stored onto diskettes allowing full spectral analysis up to 320 kHz, well above the highest frequency of interest.

To insure that the acoustic data was not biased or cut off, the recording system was tested for full fidelity prior to beginning analysis. A set of dolphinlike clicks consisting of narrow-band and wideband signals with peak frequencies centered at 60, 110, and 120 kHz was played into the system from a D to A converter operating at 1 MHz. The FFTs of the slowed and transferred signals produced by the Masscomp matched those of the original signals.

To avoid confusion with signals emitted by other dolphins in the pool, the signals recorded at the Edo-Western hydrophone were used as a time reference in the analysis of the signals recorded at the LC-10 hydrophone. Echolocation clicks ($N = 7005$) were extracted from the recordings by matching the major peaks in each channel based on the travel time between the two hydrophones (approximately 657 μ s). Signals that could not be matched were disregarded as having been emitted by another dolphin. Data generated and stored onto diskettes included an (1) oscilloscope image of the emitted signals in the sample, (2) the total number of

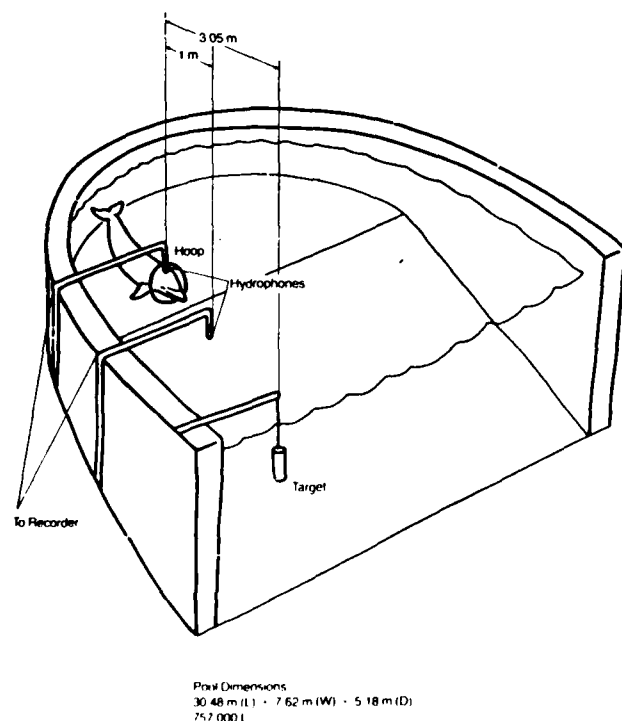


FIG. 1. Schematic diagram of the positions of dolphin, target and hydrophones during trials

clicks extracted per trial and their relative times of occurrence, (3) an average waveform based on the clicks in the sample and its frequency spectrum (Fast Fourier Transform), (4) an average FFT based on the FFTs of each click in the sample, (5) waterfall displays of the waveforms and their corresponding FFTs, and (6) an interclick interval (ICI) histogram. Peak-to-peak sound-pressure levels, 3-dB bandwidths, and signal duration were determined by measurements taken by hand from the graphic representations of waveforms and their respective FFTs.

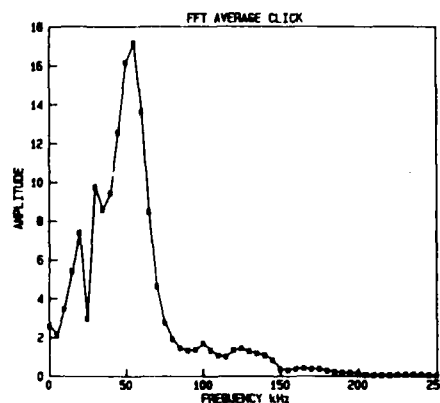
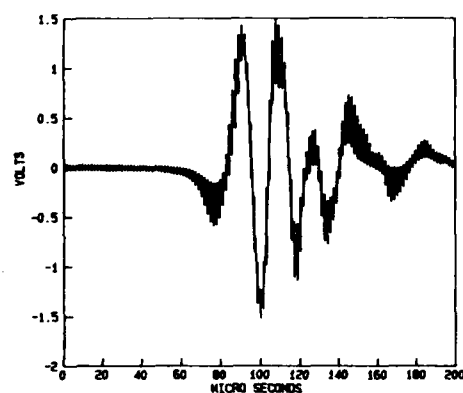
II. RESULTS AND DISCUSSION

The amplitudes, peak frequencies, 3-dB bandwidths, ICIs, and the number of echolocation clicks emitted per re-

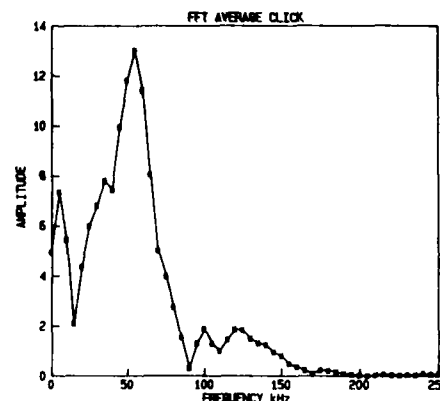
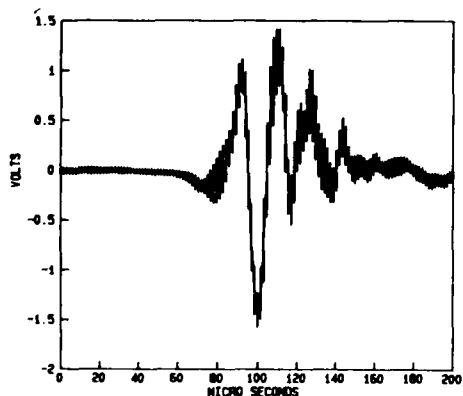
corded trial were examined. Hooded and baseline conditions were compared for any observable strategy that may have been employed in the emission of outgoing signals by the dolphin in order to compensate for the attenuation of incoming signals at its lower jaw.

The echolocation signals recorded typically had durations of approximately 140–150 μ s, peak frequencies between 30 and 55 kHz, 3-dB bandwidths of 30–50 kHz, and peak-to-peak sound pressure levels (SPLpp) between 170 and 180 dB *re*: 1 μ Pa at 1 m, with few exceptions. The average waveform and its corresponding FFT of a representative trial from each of the three conditions tested are displayed in Fig. 2. Diercks *et al.* (1971) reported a peak frequency of 35 kHz and Evans (1973) reported a peak frequency range of

Baseline



Control Hood



Experimental Hood

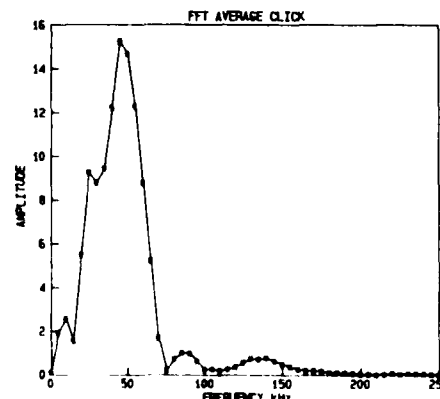
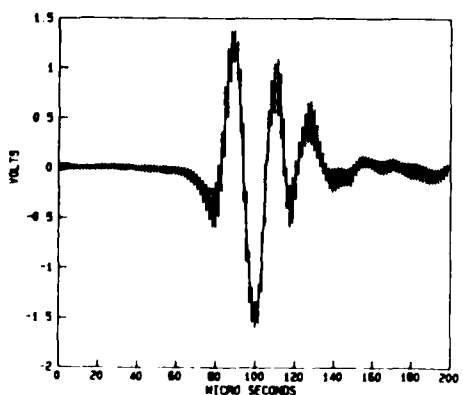


FIG. 2. An average waveform derived from all of the clicks in a trial and its frequency spectrum for each of the three conditions tested. Bars on the waveforms indicate the range (i.e., mean \pm 1 s.d.) of voltage observed in the sample.

35–60 kHz for *Tursiops truncatus* also in concrete pools, as opposed to 110–130 kHz in open water reported by Au (1980).

Mean values for SPLpp, peak frequency, 3-dB bandwidth, and the number of echolocation clicks extracted from each sample in the baseline, control and experimental conditions are displayed in Figs. 3–5, respectively. Variations in the mean number of clicks occur in the control and experimental conditions. The number of clicks follows a “W” pattern over sessions in both conditions with a greater increase in number and ICIs of shorter duration in the experimental condition.

Norris *et al.* (1961), Norris and Harvey (1974), Au *et al.* (1986), and others have provided evidence that odontocete cetaceans emit echolocation signals from the area of the forehead above the line of the gape of the mouth and that those signals are focused forward in a directional manner. If the signals emitted by dolphins during echolocation originate in the larynx and are radiated in an omnidirectional field without being focused forward through the melon as has been previously suggested (cf. Purves and Pilleri, 1983), then the placement of hoods on the dolphin’s lower jaw in this experiment should have blocked and distorted its emitted signals. The waveforms and their respective frequency spectra displayed in Fig. 2 indicate that the emitted signals were unaffected by the presence of either hood at the lower jaw. In examining Fig. 2, it is difficult, at best, to determine which of the three waveforms presented correspond to a particular condition without the benefit of appropriate identification. Clearly, the dolphin was able to emit useful echolocation signals in all three conditions, and those signals were being emitted from a site above the line of the gape of the mouth. These data further support the assumption that the hoods were, in fact, affecting the reception of echolocation signals and not their emission.

Several investigators have provided evidence that dol-

phins exert control over the characteristics of their emitted signals as they echolocate (Turner and Norris, 1966; Norris *et al.*, 1967; Norris *et al.*, 1972; Evans, 1973; Au, 1980; Moore and Pawloski, 1991). It had been anticipated that the dolphin in this experiment would change its outgoing echolocation signals, particularly with respect to sound-pressure level and repetition rate, to compensate for the attenuation of incoming signals at the lower jaw. Changes did seem to occur in the temporal parameters in terms of the number of emitted clicks and the duration of the ICIs. The spectral parameters, however, appear stable across conditions. It is likely that they did not vary due to the limitations imposed by the environment, a concrete pool, on the range of useful energy in the emitted clicks.

Before completing this experiment, Brill (1988a) suggested the possibility that the dolphin was using shorter bursts composed of fewer clicks and ICIs of longer duration in the hooded conditions, as compared to the baseline condition. The complete data from this experiment, however, indicate a lower average number of clicks per trial in both of the hooded conditions with a shorter ICI only in the experimental condition.

An echolocating dolphin typically increases its click repetition rate and, conversely, decreases the length of ICIs as it homes in on its target (Busnel and Dziedzic, 1967; Evans and Powell, 1967; Norris *et al.*, 1967; Morozov *et al.*, 1972). Norris (1964) suggested that the repetition rate may be related to the degree of discrimination desired by the dolphin at any given moment. Au *et al.* (1982) pointed out that interclick intervals almost always exceed the two-way transit time to the target implying that the echo from one click is received by the dolphin before the next click is emitted. Murchison (1980) proposed that interclick intervals used by echolocating odontocetes are behaviorally controlled by the animal and are relative to its “search image”; the returning signal expected from a familiar target.

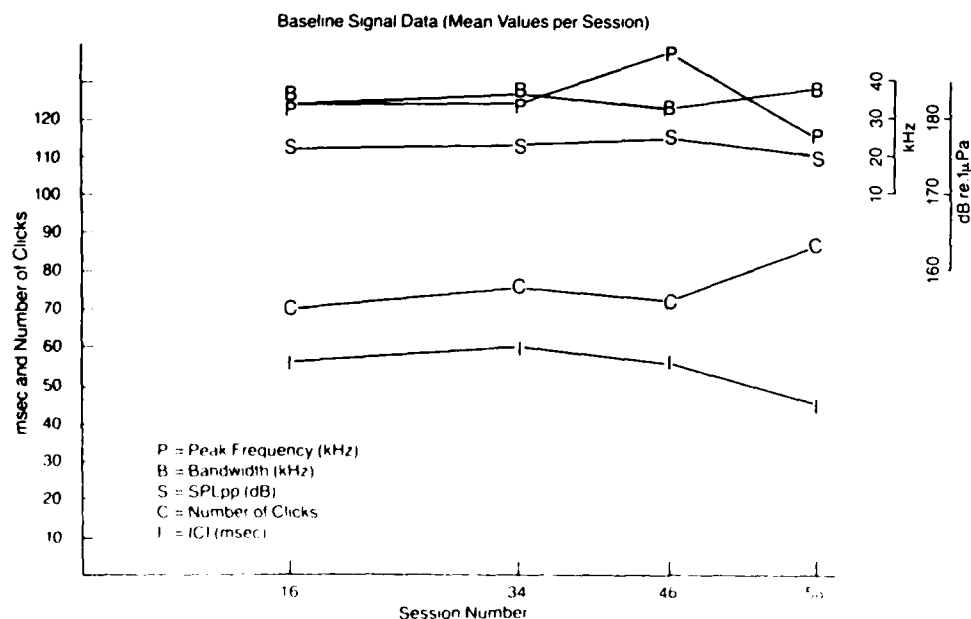


FIG. 3. Mean values for peak frequency, 3-dB bandwidth, peak-to-peak SPL *re* 1 μ Pa, and number of clicks per trial plotted as a function of time for the tape recorded sessions in the baseline condition. Values for time and number of clicks are read from the scale at the left. Values for frequency and source level are read from the respective scales at the right.

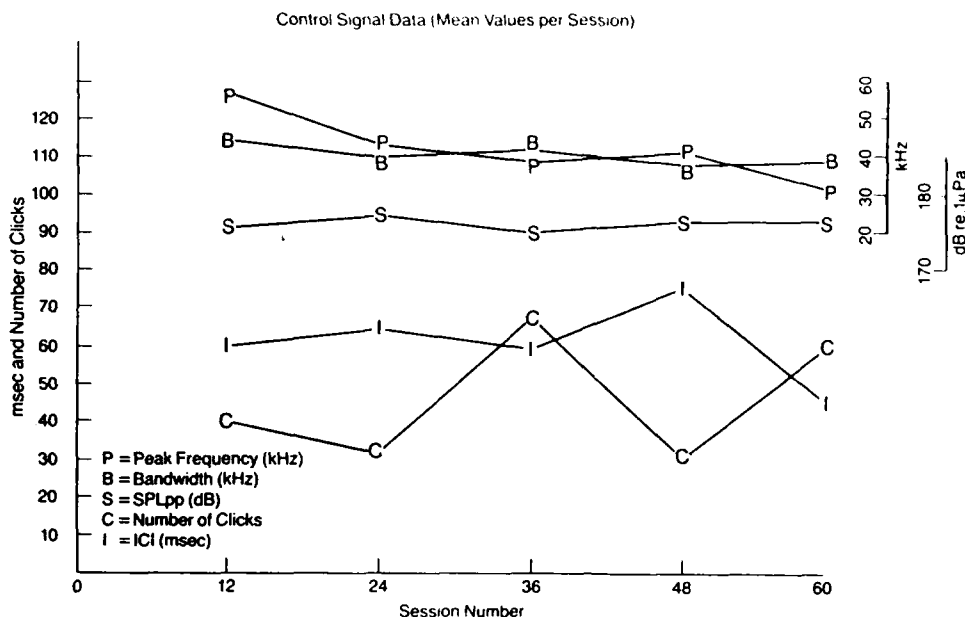


FIG. 4. Mean values for peak frequency, 3-dB bandwidth, peak-to-peak SPL *re* 1 μ Pa, and number of clicks per trial plotted as a function of time for the tape recorded sessions in the control condition. Values for time and number of clicks are read from the scale at the left. Values for frequency and source level are read from the respective scales at the right.

An ICI can be defined as the sum of two-time components; the two-way transit time for sound between the dolphin and its target, plus the processing time (cf. Morozov *et al.*, 1972), during which information contained in the incoming signal is being processed by the central auditory system. There has been a good deal of variation reported in the length of the information processing component of ICIs. Au *et al.* (1974), for example, reported mean values as high as 50 ms over the two-way transit time in ICIs they measured for targets presented at a distance of 77.8 m in open water. In our experiment, the two-way transit time between the dolphin and the target was always 4 ms and the two-way transit

time between the dolphin and the far end of the pool was always 30 ms. Considering those factors and a review of the ICI histograms for the trials recorded in this experiment, 120 ms was selected as the acceptable maximum ICI. All ICIs greater than 120 ms were assumed to be the intervals between trains of clicks and were excluded from the samples.

Histograms using time-bins of 10 ms were generated for each trial and compiled into a single histogram for each condition. The cumulative histograms are displayed in Fig. 6 in terms of the percent of all ICIs per condition falling into each 10 ms bin. The respective values for the minimum ICI, mean ICI, and the percent of ICIs falling below 50 ms are also

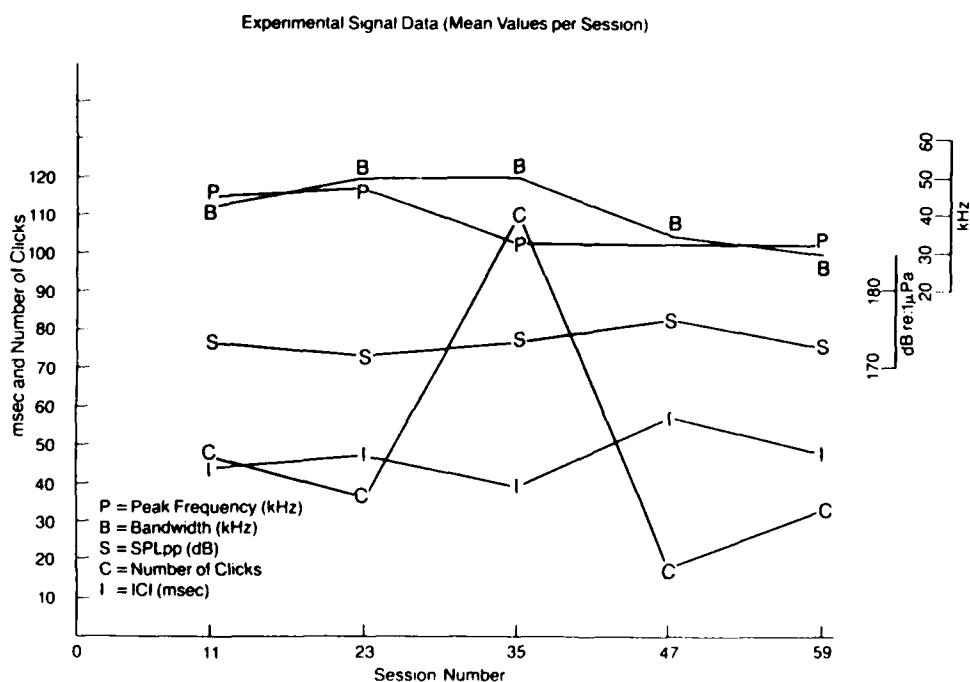


FIG. 5. Mean values for peak frequency, 3-dB bandwidth, peak-to-peak SPL *re* 1 μ Pa, and number of clicks per trial plotted as a function of time for the tape recorded sessions in the experimental condition. Values for time and number of clicks are read from the scale at the left. Values for frequency and source level are read from the respective scales at the right.

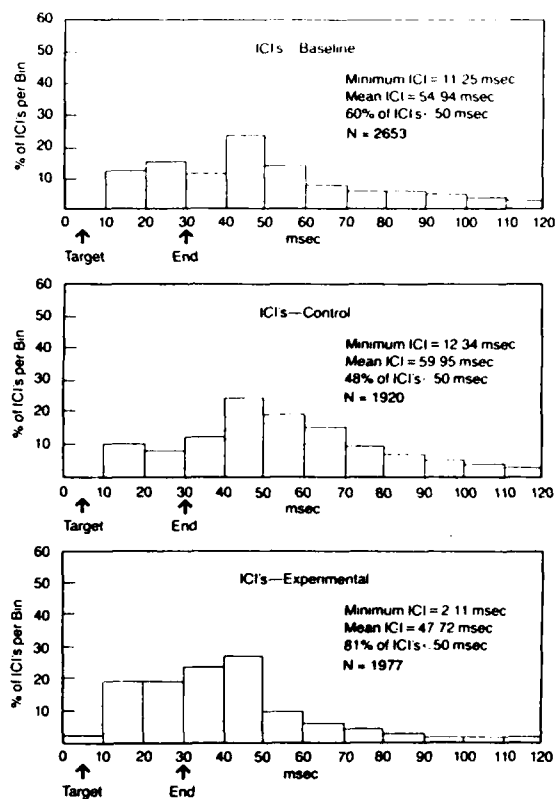


FIG. 6. ICI histograms for the baseline, control, and experimental conditions represented in terms of the percent of ICIs that fell into each 10-ms bin. Arrows indicate two-way transit times for the target and the far end of the pool. Values for the minimum ICI, mean ICI, percent of ICIs less than 50 ms, and total number of ICIs for each condition are shown.

listed in the figure. The ICI distributions for all three conditions peak at 40–50 ms. The distributions for the baseline and control conditions appear to be similar. The distribution for the experimental condition appears to be slightly skewed with 81% of the ICIs falling below 50 ms. It is the only condition with ICIs in the 0–10 ms bin and a minimum ICI value, 2.1 ms, less than the two-way transit time to the target.

The fact that the ICI histograms presented in Fig. 6 all show peaks in the 40- to 50-ms bin suggest that the dolphin relied most frequently on an interval that allowed for the return and processing of all returning echoes. An ICI of 40–50 ms would allow for both the greatest two-way transit time in the test environment, 30 ms for the far end of the pool, and a reasonable length of processing time.

The dolphin's performance in the experimental condition never improved over time. We propose that the ICIs of shorter duration evident in the skewed distribution for that condition (see Fig. 6) and the somewhat lower average number of clicks are indicative of a reaction to the absence of some anticipated information or search image. We believe that the acoustic information in the returning echoes available to the dolphin in the baseline and control conditions was

being obscured in the experimental condition due to the use of the sound-attenuating hood.

III. SUMMARY

Brill *et al.* (1988) demonstrated that the use of a sound attenuating covering over the lower jaw of a dolphin significantly hindered its ability to echolocate. Investigation of the echolocation signals recorded during that experiment indicate the following. (1) Outgoing echolocation signals did not appear to be affected by the placement of neoprene coverings, or hoods, over the lower jaw of the dolphin. Therefore, those signals were transmitted from a site above the line of the gape of the mouth. (2) Click repetition rates were only slightly lower in the hooded conditions. (3) Interclick intervals (ICIs) were noticeably shorter in duration in the experimental condition. The use of fewer clicks combined with shorter ICIs in this condition was most likely due to the attenuation of returning echoes. (4) Spectral parameters (amplitude, peak frequency, and bandwidth) of the outgoing signals showed little variation. Overall, the data support the model of cetacean echolocation proposed by Norris (1964, 1968, 1969).

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